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The ethological deconstruction of fear(s)

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Abstract

The natural world presents a myriad of dangers that can threaten an organism's survival. This diversity of threats is matched by a set of universal and species specific defensive behaviors which are often subsumed under the emotions of fear and anxiety. A major issue in the field of affective science, however, is that these emotions are often conflated and scientists fail to reflect the ecological conditions that gave rise to them. I attempt to clarify these semantic issues by describing the link between ethologically defined defensive strategies and fear. This in turn, provides a clearer differentiation between fears, the contexts that evoke them and how they are organized within defensive survival circuits.

Introduction

Charles Lyell's *Principles of Geology* [1], which proposed the theory that the Earth's surface was shaped by slow incremental changes, was a key inspiration for Darwin's 'On the Origin of Species' [2]. Analogous to Lyell's geological theory, the idea that complex nervous systems emerged from simpler organisms via similar incremental processes fit with both Darwin's and Lamarck's theories that the inheritance of phenotypes are the direct result of the changes in the organism's ecology. Reaching across the modern scientific disciplines of paleobiology, ethology and neuroscience, there is agreement that when one views the human brain through the lens of evolution, our brains have gone through the same gradual processes, and in turn, that we possess some of the same phyletic neural structures and innate reactions that our mammalian cousins use to survive. It has also become clear, however, that the human neural circuits are unique. This uniqueness comes from our highly expanded cortex, which includes a plastic machinery that allows us to probe near and distant futures [3], to consciously experience emotions (i.e. feelings) [4] and cognitively regulate them [5]. The current consensus is that older neural structures combine with newer ones to form a highly complex circuitry that has evolved to maximize fitness by reacting to, and anticipating, predatory, social and homeostatic threats [6^{●●}].

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While few scientists dispute that animal and human brains have evolved similar circuits to combat a variety of ecological threats, there is controversy. At the forefront of this debate is LeDoux's 'Survival Circuits Theory' [7] which states that affective scientists should rethink the notion that emotions, such as fear, are similar between humans and other animals. LeDoux proposes that 'fear' is a cognitive process associated with higher order 'feelings' of terror or horror. Thus, fear comes about via conscious experiences and emerges from brain structures involved in what LeDoux calls general networks of cognition [4]. This is differentiated from defensive survival circuits, which are involved the first line of defense against pre-dators and result in innate defensive reactions. Defensive survival circuits contribute to cognitive fear, but do not constitute fear. Thus, given the conscious and subjective nature of fear, only defensive survival circuits can be studied in other animals. This distinction has vigorously been debated [8], yet this debate opens up a new opportunity for affective scientists to reconsider how to define and investigate fear.

In this article, I argue that to successfully map human and animal defensive survival circuits, researchers should first investigate the ecological conditions that evoke them. This approach also provides clearer definitions of fear and anxiety, which are often used interchangeably, conflated and not tied to a well-defined set of natural conditions. In turn, describing the ecological conditions that map onto different level of predation, we find that different patterns emerge in behavior, computations, strategies, psy-chological states that have distinct and overlapping defen-sive survival circuits. This is not a new concept. Theorist such as Jeffery Gray have proposed that a central question when studying fear is 'what are the conditions that give rise to fear' [9] (pp. 8). Behavioral ecologists and the like, have also considered these conditions, most prominently captured in Fanselow and Lester's 'Threat Imminence Continuum' [10] and Lima and Dill's 'Predator-Prey Interaction' model [11]. By investigating how animals evade and combat threats across a variety of natural contexts allows researchers to elucidate survival strategies and how these are modulated by other survival behaviors such as mating, sustenance and protection of progeny [12,13●]. Understanding these strategies allows one to create better computational models and consequently create a better understanding of the defensive survival circuits that have evolved within and across species. Therefore, to understand fear, and potentially other emotions, one must first consider the evolutionary and eco-logical conditions that give rise to them.

The fuzzy semantics and measurement of fear

Stanley Rachman has stated that 'although the word fear is used without difficulty in everyday language ... problems arise when it is used as a scientific term' [14] (pp. 11). LeDoux [15●●] stays close to the common usage of the term by suggesting that: 'fear' can be described as 'the feeling that invades your conscious mind when you are in danger' (pp. 303). Given that fear is a conscious operation, it is common for affective scientists to directly probe a subject's fear state by recording their subjective appraisal or state of mind. However, this has been problematic as Rachman points out that 'subjective reports of fear also tend to be of limited value in assessing the intensity of the experience because of the difficulties involved in translating phrases such as 'extremely frightened', 'terrified' and 'slightly anxious' into a quan-titative scale with stable properties' [14] (pp. 12). This criticism along

with the inability to probe ‘fear as a feelings’ in animals, has led others to consider other measures of fear. For example, Mower [16], Bolles [17] and Fanselow [10] have operationalized fear as a reactive response to danger characterized by, for example, freezing or fleeing, and do not consider the subjective cognitive baggage that accompanies such behaviors. This makes sense when studying rodents, however, as LeDoux [7] points out, fear responses are species specific despite the fact that the circuitry may be species general and defensive behaviors may only reflect the motivation state of the organism.

To make matters confusing, fear and anxiety are often conflated. For example, Rosen and Schulkin [18] define normal fear as ‘both the adaptive fear and anxiety state’ and further state that fear is a response to a ‘potentially dangerous event’. This conflation and confusion between fear states is important to address, because until there is consensus on semantics as well as the conditions by which to evoke and measure fear, we can never have consensus on the neural circuits associated fear and anxiety, and we will ultimately fail when trying to understand how these are disrupted in patients suffering from affective psychopathology [19]. How do we remedy this? One approach is to reverse engineer the problem and disassemble fear states by the variety of ecological contexts that they evolved for (Figure 1). As I will discuss, this approach allows one to create unambiguous definitions and experimental paradigms.

Fear and anxiety in the natural world

Julian Huxley [20], and later Niko Tinbergen [21], proposed that one must consider the ultimate function of behavior or ‘why’ behaviors relate to survival of the species. While adaptationist accounts, which propose that evolutionary acts as an optimizing agent, have been criticized [22], they do provide a conjectural window into the ecological conditions that drive survival behaviors. As Stephens and Krebs [23] point out: ‘asking what a machine is for helps the engineer understand how it works.’ Further, adaptationist accounts become testable questions when behaviors are examined in the ecological niche of the species and how these behaviors relate to survival (e.g. how Galapagos finches’ beaks relate to feeding behavior). O’Keefe and Nadel [24] suggest that one should examine the natural world before experimentation. Likewise, to understand fear, one must first consider the natural conditions by which survival behaviors are elicited (Figure 1).

The ethological atomization of fear

Fear takes many forms from the quick reaction to proximal danger, to the slow dread associated with a looming distant threat [6,25]. When defined this way, it is clear that both the immediate reactions and sustained conscious sensations of fear emerge from different neural computations, thereby supporting LeDoux survival circuitry theory [7]. This is analogous to other neural processes, such as those that support visual attention, where attention can be consciously and volitionally guided (top down) or reflexively captured by a salient stimulus (Bottom up). These two types of attention are supported by overlapping and non-overlapping neural circuits (e.g. prefrontal versus parietal neurons [26]), both with the goal of detecting salient stimuli. Given that one goal of fear is to detect and respond to environmental threats, one could support the idea for an analogous set of processes (c. f.

[27]). The evidence for such a separation of fears and anxieties is abundant. However, I believe that it is unlikely that the field of behavioral neuroscience will give up the term ‘fear’ to describe innate behavioral reactions such as freezing and flight [28]. Therefore, I sub-categorize fear and anxiety into several forms: (i) reactive fear, (ii) cognitive fear, (iii) anticipatory anxiety, (iv) encounter anxiety. Because of space, emphasis is placed on (i) and (ii).

Reactive fear

Reactive fear is the core of LeDoux’s defensive survival circuits and is evoked when the organism is under immediate attack (i.e. circa-strike defense; see Figure 2). Here I define reactive fear as ‘a quick, phasic, mostly unconsciously and loosely coordinated reaction in response to an imminent threat that is, or perceived to be, directed toward the organism and where there is little time to cognitively comprehend the danger of the situation’. Reactive fear is tightly linked to rapid interoceptive signals [29], is model-free and associated with what McNaughton and Corr called ‘external risk assessment’ or defensive decisions that are evoked by some external threat stimulus [30●]. Reactive fear is characterized by a set of overt defensive behaviors including, fight, flight and freezing and in most cases, results in fast, yet coordinated reactions that are observed across species. The goal of this type of fear is to make quick and dirty survival decisions via a set of basic fear circuits that evolved to evade and combat ballistic attack by predators. Their ubiquity supports their success as survival strategies, their genetic programming and their automaticity. The skeptic might suggest that what I call reactive fear is conflated with the overt behavior (e.g. freezing or flight) and may not involve fear at all. This is justified, mainly because the majority of studies have been conducted on rodents and rodents cannot tell us how they ‘feel’! The behaviorist’s response is that in this case, (REACTIVE) FEAR IS THE OVERT BEHAVIOR. We can have confidence, however, that reactive fear behaviors also come with changes in the autonomic nervous systems (e.g. piloerection, heart rate increases), are disturbing to the animal by a proxy of cues (shivering, distressing vocal cues) and can result in long-term psychological symptoms.

Cognitive fear

In humans, cognitive fear is evoked when the organism is under direct threat, but has time to organize and strategize escape as well as subjectively contemplate the situation [31]. Further, reactive fear is followed by cognitive fear, but may also precede reactive fear and even evoke it (Figure 2). Cognitive fear is defined here as ‘a conscious feeling of terror, which results from the presence of a threat, that is, or perceived to be, directed toward the organism, and where there is not only time to strategize escape, but also comprehend the forbidding nature of the situation’. Contemporary theorist such as Davis *et al.*, proposed that ‘humans are endowed with a cognitive system that enables symbolic representation of aversive experience, and the knowledge of future aversive events is sufficient to create a threatening context’ [32] (pp. 106). This allows the organism use cognitive avoidance strategies. Others have linked it to an ‘internal risk assessment’ connected to higher order cognitive systems such as memory scanning, rumination, evaluation [30●] and is model-based (Qi *et al.*, [33]). An example of applying paradigms from behavioral ecology to

understand decision making under fast and slow predatory attack. Results support the theory that reactive fear circuits are evoked when there is little time to strategize escape. Conversely, cognitive fear circuits come online when the subjects have time to make adaptive decision using internal risk assessment.).

Cognitive fear sits closer to older theories by William James and Carl Lange and Schachter and Singer's 'Cognitive Appraisal Theory' as well as more contemporary theories such as Feldman-Barrett's 'Emotion Construction Theory (ECT [34]) and LeDoux and Pine's recent 'Two Stage Model' of fear. Such subjective and conscious experiences can be measured and even manipulated in humans. For example, Schachter and Singer demonstrated how the cognitive system is plastic by showing that: 'Given a state of sympathetic activation, for which no immediately appropriate explanation is available, human subjects can be readily manipulated into states of euphoria, anger, and amusement' [35] pp. 396). Feldman-Barrett's ECT [34] fits with a cognitive model of fear, but not reactive fear, which I argue is a natural kind of emotion, is universal and has a dedicated circuit. This does not omit the possibility that reactive fear is a product of an integrated survival circuitry.

Disentangling reactive and cognitive fears from anticipatory and encounter anxiety

I differentiate anxiety from fear by the properties, and the perceived intensions, of the threat as captured in the threat imminence continuum (Left panel; Figure 2). Anxiety can occur in safe or pre-encounter conditions via 'what if' cognitions [36] as well as during actual encounters with distal non-attacking threat. This results in a specific type of anxiety I call, firstly, 'Anticipatory Anxiety' or an 'apprehension of danger with the absence of direct threat, but the possibility, or uncertainty, of encountering the threat in the future'. Anticipatory anxiety is adaptive, because it results in anticipatory avoidance (e.g. movement away from a location where one could potentially encounter threat in the future) and captured by place aversion. This type of anxiety motivates the organism to simulate potential encounters with a threat thereby evoking precautionary behaviors, such as alertness, environmental surveillance and what can be called pre-encounter avoidance (i.e. avoiding threat before it is encountered). Anticipatory anxiety switches to a different type of anxiety when a threat is present as in the post-encounter threat (i.e. detection of a threat, but no interaction), which results in what may be called, secondly, 'Encounter Anxiety' or 'the apprehension of danger without direct threat, but the possibility of the threat directing its focus toward the organism resulting in increased urgency to avoid the situation'. This is typically experienced when the threat is distal, and results in freezing or non-urgent avoidance (coordinated movement away from a distal threat; see [25]. If the threat is proximal (but not attacking), it may further result in urgent avoidance and another type of anxiety. In this situation, these encounter anxiety circuits may merge with cognitive fear systems, but are distinguished by survival behaviors such as freezing and urgent avoidance, which resembles coordinated escape (Figure 2). On a cognitive level, the major difference between fear and anxiety is directly related to how much time the organism has to think. In general, anxiety in its different forms attempts to reduce the likelihood of encountering a threat.

Back to defensive survival circuits

LeDoux's theory [7] proposes that survival circuits evolved for multiple survival behaviors where the goal of the nervous system is homeostasis between energy management, reproduction needs, defense, fluid balance and thermoregulation. There is little disagreement that these are all important in survival, but what is disputed is whether there are dedicated circuits for each of these needs or if they are part of the same circuitry (e.g. [37]). Here, I just focus on defensive survival circuits and my view on this topic is that the way scientists and lay persons use the term fear (and anxiety) confuses its evolutionary purpose, its complexity and the neural circuits that support this emotion(s). As described above, my antidote to this problem is to consider the ecological contexts that give rise to a set of survival strategies and behaviors. For example, recent work from my lab, has supported this 'cognitive' and 'reactive' fear differentiation of defensive survival circuits by showing that fast escape decisions are elicited by the PAG, regions involved in reactive flight. Conversely, slower escape decisions rely on the hippo-campus, posterior cingulate cortex and prefrontal cortex, a circuit implicated in behavioral flexibility and internal risk assessment [30]. This study does not measure the complexity of fears, but shows for the first time how one can separate the survival circuits based on ethologically-defined contexts (Figures 1 and 2). Along with anatomical models, (e.g. Price's medial PFC network), these results show how circuits are potentially overlapping, interconnected, yet are differentially evoked for different types of threat, therefore supporting the survival circuits hypothesis [7].

Concluding remarks and new directions

Affective scientist should feel free to contemplate the adaptive functions and phyletic differences across species. This should also include a thorough understanding of fears in the natural world, what contexts evoke them and how these are species specific and species general. Only then can we overcome the opaque semantic issues that plague the study of fear. To facilitate this, affective scientists studying the human defensive survival circuits need to push for a paradigm shift in experimental methods [13] with a drive toward the use of ecologically valid approaches such as the use of real threat stimuli (e.g. [38–40]). Some researchers of fear are already proposing a move away from fear conditioning to naturalistic approaches that involve avoidance paradigms and decision-making with a larger rapporteur [37]. The first example of this have occurred in rodents [41] and humans (Qi *et al.*, unpublished data, An example of applying paradigms from behavioral ecology to understand decision making under fast and slow predatory attack. Results support the theory that reactive fear circuits are evoked when there is little time to strategize escape. Conversely, cognitive fear circuits come online when the subjects have time to make adaptive decision using internal risk assessment). Researchers [14] have also proposed that one should also attempt to measure four aspects of the, (i) the subjective, internal assessment or cognitive experience (see [42]), (ii) associated physiological, including, but not limited to, neurobiological and endocrinological changes, (iii) the external assessment and outward behavioral expression of the fear including to avoidance or escape behaviors and any propensities that alter (i)–(iii) including (iv) individual differences in environment, genetic and developmental traits [43,44]. While all these measurements of fear are often incongruent

with each other [4], it is this incongruence that supports a differentiation between fear states and evidence that they evolved under different contexts of danger.

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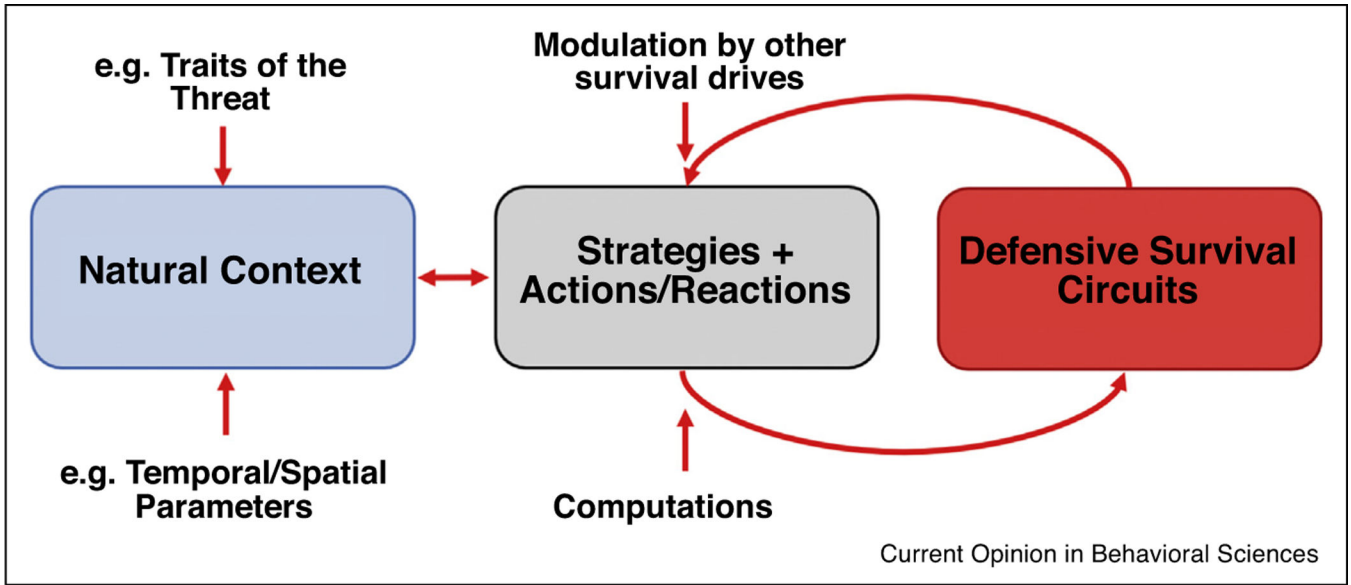
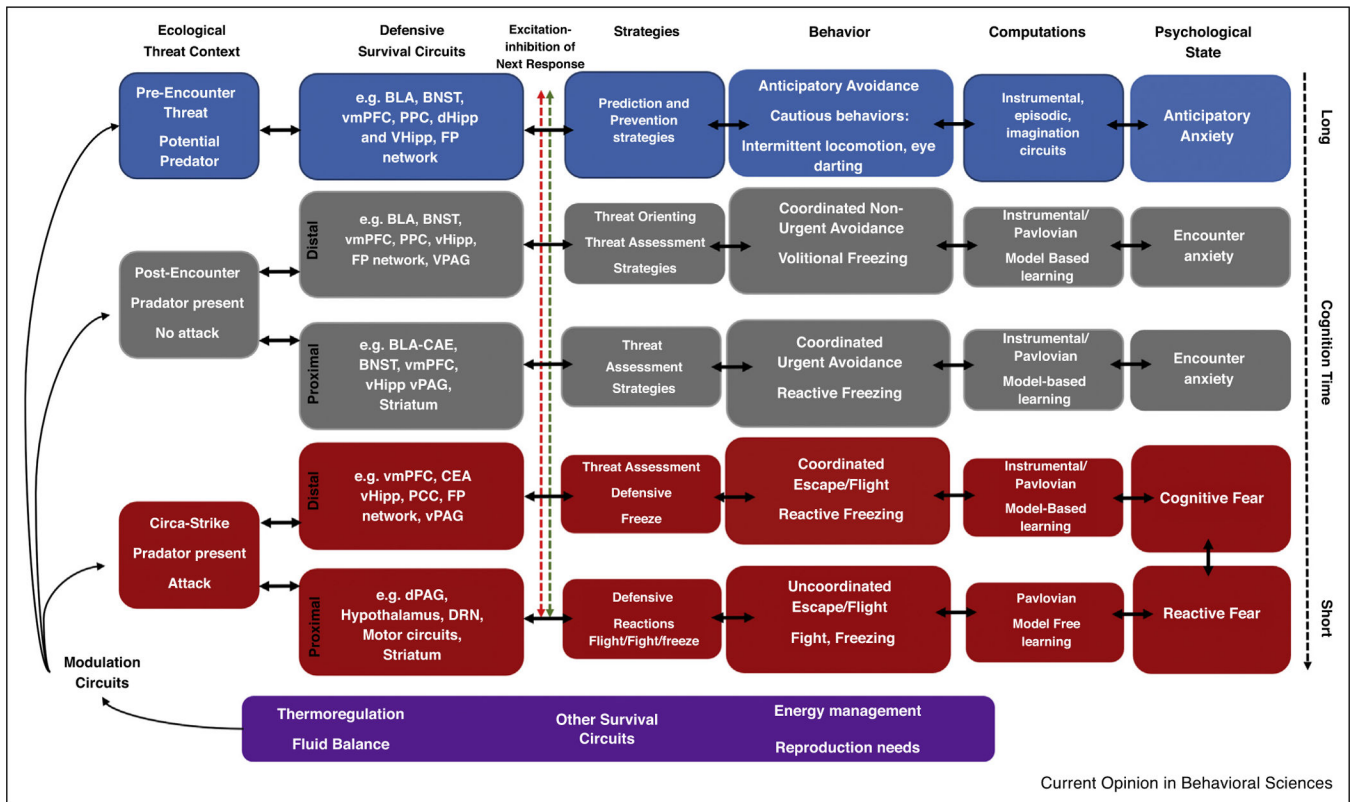


Figure 1. A simple flow model showing the links between the natural world, including the traits, spatial and temporal properties of the threat and the cognitive/behavioral strategies and computations that have evolved for successful escape and avoidance of danger. Finally, these strategies are embedded in defensive survival circuits.



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Figure 2.

An example of how levels of predatory imminence map onto defensive survival circuits. The left panel illustrates several of Fanselow and Lester’s levels of ‘predatory imminence’ that extend from: (i) pre-encounter context, which is the time period where there is a risk of interaction with a predator, but no predator is actually present; (ii) post-encounter threat is when a threat is detected, but there is no direct interaction between the prey and predator (e.g. the predator has not yet detected the prey) and (iii) circa-strike threat is the stage where the predator starts to attack the prey with the intention of capture and consumption [11,45]. These levels of threat imminence are also played out in the context of homeostatic threats such as starvation, and energy needs and have their own distinct strategies, behaviors, computations and psychological states [6●●]. Further, these levels of threat and their defensive responses are modulated by other survival circuits [7]. The red and green dotted line refers to the excitation or inhibition of other defense responses. Note, for simplicity, other physiological responses (e.g. autonomic and endocrine systems) are not in the model.